

***Clavaria cystidiata* sp. nov. from India**

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ABSTRACT—A new species, *Clavaria cystidiata*, was collected and described from Kerala State, India. The species is proposed as new based on morphological and molecular evidence. *Clavaria cystidiata* differs from other closely related *Clavaria* species by its garlic smell, yellowish basidiomata, clamp connections at the base of basidia, and by the prominent presence of versiform cystidia. Sequence analyses of the nuclear rDNA internal transcribed spacer (ITS) region supports phylogenetic separation of *C. cystidiata* within *Clavariaceae*.

KEYWORDS—*Agaricomycetes*, alliaceous, biodiversity, *Agaricales*, coral fungi

Introduction

Clavaria Vaill. is a basidiomycetous genus, comprising about 178 described species (Roskov & al. 2020). The genus has a cosmopolitan distribution. Representatives grow primarily as saprobes and (exceptionally) as associates of soil algae and ericoid plants (Corner 1950; Englander & Hull 1980, Olariaga & al. 2015). Basidiomata are simple (rarely branched), cylindrical to club shaped, and whitish, yellow, orange, pink, violet, or brown to black in color. Holobasidia bear hyaline spores. Characteristics of the basidia, hyphae, and presence and location of clamp connections have been used in infrageneric classifications.

Basidiomatal color has been used both as a key taxonomic character for delimiting species and informally grouping species within the genus (Corner 1950, 1970; Knudsen 1997; Petersen 1978, 1988; Roberts 2007; Kautmanová & al. 2012). Kautmanová & al. (2012) analyzed the phylogeny of dark *Clavaria* species (with grey, brown, and black basidiomata) using LSU nrDNA sequence data. Olariaga & al. (2015) studied yellow *Clavaria* species with clamped basidia

and inferred species relationships based on ITS and LSU nrDNA sequence analyses.

Similarly, the distinctive smell of basidiomata has served as a distinguishing taxonomic character in the genus. Basidiomata of some *Clavaria* species are known to emit a distinctive alliaceous smell, and Petersen (1988) used garlic smell as one identifying character in his keys to the New Zealand clavarioid species. *Clavaria falcata* Pers., *C. foetida* G.F. Atk., *C. fuscata* Oudem., and *C. redolealii* R.H. Petersen are the four known garlic-smelling species of *Clavaria*.

During an exploratory survey of the clavarioid fungi of Kerala, India, we encountered basidiomata of a garlic-smelling yellowish clavarioid fungus. Detailed examination revealed this collection as unique from all other described *Clavaria* species. Details of our morphological and molecular examination accompany the proposal of a new species. A key to *Clavaria* species reported from India is also provided.

Materials & methods

Morphological characterization

Fruit bodies were collected from Kerala State, India, during August 2017. Fresh material was examined macroscopically and tested with FeCl_3 and KOH. Dried materials were examined microscopically and stained using aqueous solutions of 3% phloxine and 1% Congo red mounted in 5% aqueous KOH. Twenty basidiospores were measured to calculate dimensions, mean, and standard deviation for length and width, range of spore quotient (Q , length/width ratio) and its mean value (Q_m). Basidiospore reactivity to Melzer's reagent and cotton blue was noted. The holotype was deposited at the Central National Herbarium, Kolkata, West Bengal, India (CAL), and an isotype was deposited at the Zamorin's Guruvayurappan College Herbarium, Kozhikode, Kerala, India (ZGC).

Molecular characterization & phylogenetic analysis

Genomic DNA was extracted from dried basidiomata, using the procedure of Izumitsu & al. (2012). The ITS region was amplified by PCR using primers ITS1F and ITS4 (Gardes & Bruns 1993, White & al. 1990). PCR product was purified using ExoSAP-IT treatment and sequenced using BigDye Terminator v3.1. The newly generated sequence was deposited in GenBank (www.ncbi.nlm.nih.gov) with accession number MK751792.

The newly generated sequence was subjected to a BLAST search in the GenBank nucleotide database for finding taxa with close sequence similarity. A data matrix was constructed with the newly generated sequence and ITS sequences retrieved from GenBank of 47 representative sequences in *Clavariaceae* (TABLE 1). All *Clavaria* species with ITS sequences available in GenBank were included in the dataset.

TABLE 1. Taxon and GenBank accession numbers for the ITS sequences used in phylogenetic analyses.

TAXON	GENBANK NO.	STRAIN/HERBARIUM NO.	LOCATION
<i>Clavaria acuta</i>	AY228353	F14294	—
<i>Clavaria amoenoides</i>	MF972891	AMB018217	Italy
<i>Clavaria argillacea</i>	KC759438	K(M)126733	England
<i>Clavaria asterospora</i>	KC759440	BIO-Fungi 12390	Spain
<i>Clavaria atrofusca</i>	HQ606080	BRACR 13264	Norway
<i>Clavaria calabrica</i>	MF972889	ZT Myc 58697	Italy
<i>Clavaria californica</i>	HQ179660	TENN:026785	USA
<i>Clavaria citrinorubra</i>	HQ179661	TENN:040464	Australia
<i>Clavaria crosslandii</i>	KC75944	BIO-Fungi 12762	Spain
<i>Clavaria cystidiata</i>	MK751792	CAL 1769	India
<i>Clavaria falcata</i>	KC759445	AB0532	Wales
<i>Clavaria flavipes</i>	KC759451	OJ362006	Austria
<i>Clavaria flavostellifera</i>	KC759462	BRACR16695	Spain
<i>Clavaria fumosa</i>	MK427065	Zp-2225	China
<i>Clavaria fuscata</i>	KP257128	TENN065665	USA
<i>Clavaria greletii</i>	MF503244	ERRO 2014102101	Spain
<i>Clavaria greletoides</i>	MF503243	ERRO 2009070701	Spain
<i>Clavaria griseobrunnea</i>	NR158336	12566	Spain
<i>Clavaria incarnata</i>	KC759452	BIO-Fungi 12560	Spain
<i>Clavaria redolealii</i>	MF664111	PDD105311	New Zealand
<i>Clavaria rosea</i>	MK909560	TUR 201239	Finland
<i>Clavaria rubicundula</i>	MK578690	6603126	USA
<i>Clavaria sphagnicola</i>	KC759456	BRNM 747282	Czechia
<i>Clavaria tenuipes</i>	KC759457	K(M)146565	England
<i>Clavaria tyrrhenica</i>	MF972890	ZT Myc 58698	Italy
<i>Clavaria zollingeri</i>	MH016820	FLAS-F-60642	USA
<i>Clavicornia taxophila</i>	AF033344	71850	—
<i>Clavulinopsis amoena</i>	MK427063	ZP-2400	China
<i>Clavulinopsis cf. helvola</i>	KT275650	SE-2015	USA
<i>Clavulinopsis fusiformis</i>	KM248914	2718	—
<i>Clavulinopsis laeticolor</i>	EU118618	EL 8/00	Finland
<i>Clavulinopsis miyabeana</i>	MK427059	ZP.2118	China
<i>Clavulinopsis sulcata</i>	MK427060	ZP-2119	China
<i>Camarophyllopsis atrovelutina</i>	KU882900	TL2014-682591	Denmark
<i>Camarophyllopsis phaeophylla</i>	MK139805	1ERRO 2013112901	France
<i>Camarophyllopsis rugulosa</i>	NR_119896	TENN 023664	USA
<i>Camarophyllopsis atropuncta</i>	HQ662165	4G4-2010	Ireland
<i>Camarophyllopsis schulzeri</i>	GU187556	GG091005	Wales
<i>Hyphodontiella multiseptata</i>	EU118634	Ryberg 021022 (GB)	Sweden
<i>Mucronella</i> sp.	HQ533013	PDD95742	New Zealand
<i>Mucronella</i> sp.	MH409972	strain 1214	New Zealand
<i>Mucronella bresadolae</i>	DQ384591.1	F15204	—
<i>Ramariopsis flavesces</i>	NR_119913	TENN 027570	USA
<i>Ramariopsis kunzei</i>	MK616542	AMB n. 17485	Italy
<i>Ramariopsis crocea</i>	MK607557	302989	USA
<i>Ramariopsis pulchella</i>	KX812470	MCCNNU00981	China
<i>Scytinopogon havencampii</i>	NR151488	SFSU DED8300	—

Scytinopogon havencampii Desjardin & B.A. Perry (*Hydnodontaceae*, *Trechisporales*) was chosen as the outgroup taxon following Birkebak & al. (2013). There were a total of 717 positions in the final dataset. The aligned nrITS data matrix [ID: 26259] was deposited in TreeBase. DNA sequences of the ITS dataset were aligned automatically with MUSCLE in MEGA (Kumar & al. 2018) and then manually edited using the same program.

Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian analysis (BA) methods. ML analysis was done with Tamura-Nei model (Tamura & Nei 1993) in MEGA. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pair wise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. The tree with the highest log likelihood value (−16331.38) was selected. The tree was drawn to scale, with branch lengths measured in the number of substitutions per site. BA was conducted using MrBayes 3.2 (Ronquist & al. 2012). Bayesian phylogenetic inference was done with a T92+G model with discrete gamma distributed substitution rates for the sequence dataset. The best-fit likelihood model of evolution was estimated in MEGA. Multiple independent analyses were run from random starting trees for four million generations, with trees saved every 100 generations, using four chains and a burnin fraction of 0.25.

Taxonomy

Clavaria cystidiata Krishnapriya & T.K.A. Kumar, **sp. nov.**

FIGS 1, 2

MB 832680

Differs from other garlic-smelling, yellowish *Clavaria* spp. by its prominent versiform cystidia and its bi-sterigmate basidia with basal clamp connections.

TYPE: India, Kerala State, Kozhikode District, Madapally Govt. College Campus, 9.4698°N 76.5902°E, altitude 11 m, on soil, solitary and in gregarious clusters among dead and decaying leaf litter, 01 August 2017, K. Krishnapriya (**Holotype**, CAL 1769; **Isotype**, ZGCKP59; GenBank MK751792).

ETYMOLOGY: *cystidiata*, referring to the prominent cystidia, the primary distinguishing morphological character of the species.

BASIDIOMATA ≤110 mm long, ≤3 mm thick, simple, unbranched, cylindrical, solid when young becoming hollow with age; terete in cross section; apex acute, narrowing towards base; glabrous; off white to pale yellow when young, becoming yellowish when mature, dark yellow to pale orange towards the apex; context fleshy, with strong garlic odor; no positive reaction in FeCl₃ and KOH.

BASIDIOSPORES 7–10 × 5–8 μm ($Q=1.1$ – 1.5 μm, $Q_m=1.2$ μm), broadly ellipsoid, contents granulate and guttulate (primarily one single large oil droplet), smooth, thin-walled, hyaline, apiculus prominent (≤1 μm long), inamyloid, cyanophilic in cotton blue. BASIDIA 50–60 × 7–10 μm, aguttulate



FIG. 1. *Clavaria cystidiata* (holotype, CAL 1769): Basidiomata. Scale bar=10 μ m.

to multiguttulate, cylindrical to clavate with basal clamp connection, sterigmata 1–2(≤ 5) μ m long. CYSTIDIA abundant, 21–75 $\times$ 10–21 μ m, versiform (predominantly cylindrical, clavate, lageniform, broadly clavate), many with ≤ 27 μ m long apical protrusions, thin-walled, inamyloid, hyaline.

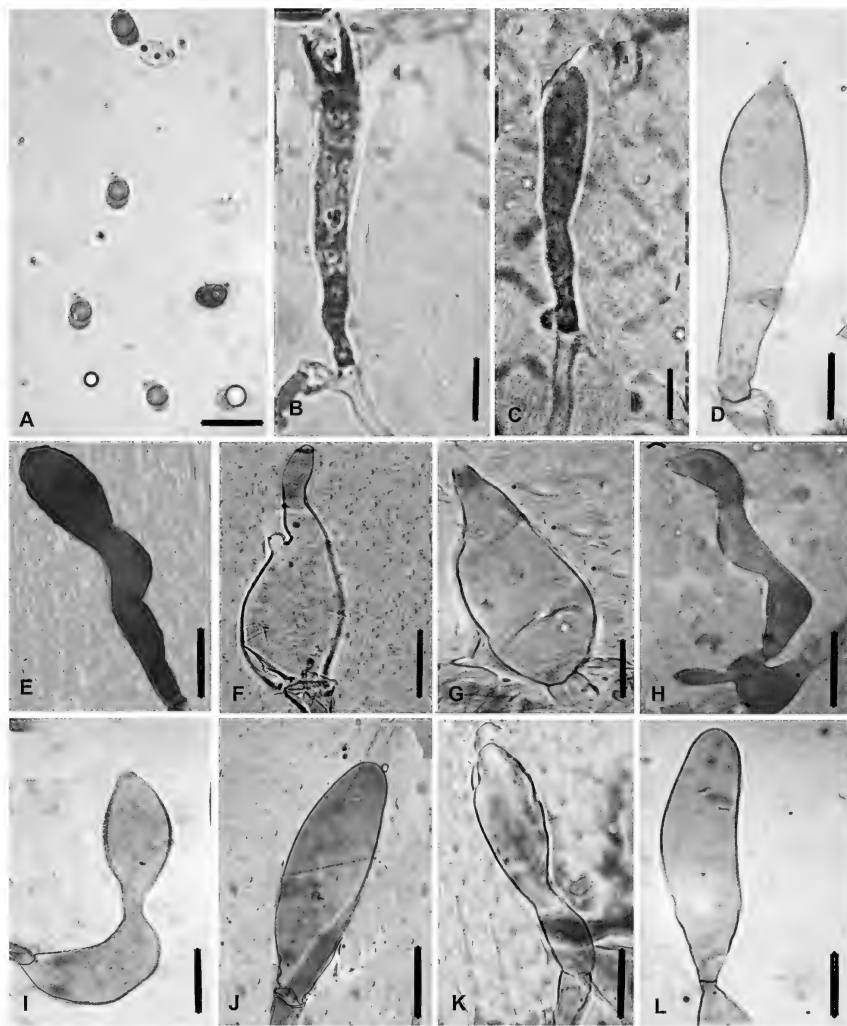


FIG. 2. *Clavaria cystidiata* (holotype, CAL 1769). A. Basidiospores; B. Basidium with sterigmata; C. Basidium with basal clamp connection; D–L. Cystidia. Scale bars: A, C= 8 μ m; B, D–L=10 μ m.

HYMENIUM 20–30 μ m wide. SUBHYMENIUM 50–60 μ m wide. CONTEXT hyphae parallel, septate, inflated, 3–25 μ m wide, hyaline to pale yellow, thin to slightly thick-walled (≤ 1 μ m), cyanophilic, inamyloid. Hyphal clamp connections absent.

ECOLOGY & DISTRIBUTION: On soil. Both solitary and in gregarious groups among leaf litter.

Molecular analysis

Sequencing of ITS region of the specimen of *Clavaria cystidiata* yielded 633 base pairs. The GenBank BLAST search of this newly generated sequence produced sequence identities of only 83% with *C. fuscata*, 80% with *C. falcata*, and 79% with *C. redolealii*, the closest BLAST hits. The ML (FIG 3) and BA (FIG 4) phylogenetic trees were congruent with respect to the majority of clades and taxa. *Clavaria cystidiata* clustered in a clade with the three garlic-smelling taxa (*C. fuscata*, *C. redolealii*, *C. falcata*) and three non-garlic-smelling species (*C. greletoides*, *C. californica*, *C. tenuipes*) with 85% ML bootstrap support (BS), and 0.86 BA posterior probability (PP) support. The new species, *C. cystidiata* resolved as sister to *C. fuscata*, receiving low (50% BS) value in the ML tree but strong (PP 1) support in the BA tree. The yellow-coloured *Clavaria* species included in the analyses—*C. amoenoides* Corner & al., *C. argillacea* Pers., *C. citrinorubra* R.H. Petersen, *C. flavipes* Pers., *C. flavostellifera* Olariaga & al., *C. inaequalis* (Pers.) Corner, *C. sphagnicola* Boud., *C. redolealii*—did not form a monophyletic group. The monotypic *Clavicornia taxophila* (Thom) Doty clustered with *Clavaria crosslandii* Cotton (84% BS, 0.94 PP). *Camarophylloopsis* species included in the study were recovered in two separate clades in both Bayesian and ML analyses. *Hyphodontiella multiseptata* Å. Strid fell into a sister clade to *Ramariopsis* and *Clavulinopsis*, forming a well-supported monophyletic group, distinct from the *Clavaria*–*Camarophylloopsis*–*Clavicornia* clade in the ML analysis. In the BA analysis, *H. multiseptata* fell into the *Ramariopsis* clade. *Mucronella* forms a distinct clade from the rest (79% BS, 0.84 PP).

Discussion

Clavaria cystidiata is recognized by its yellowish colour, strong garlic smell, basal clamp connection in basidia, presence of cystidia, large spores, and inflated hyphae. The presence of strong garlic odor and prominent cystidia are key characters which differentiate *C. cystidiata* from other yellow coloured *Clavaria* species. Corner & al. (1956) proposed a yellow *Clavaria* species, *C. amoenoides* from India. Its yellow colored basidiomata show similarity with *C. cystidiata* macroscopically but the absence of clamp connection at the base of basidia, absence of cystidia, and the absence of garlic odor (Thind 1961) makes it different.

Clavaria cystidiata closely resembles *C. fuscata*, *C. foetida*, *C. redolealii*, and *C. falcata* morphologically (TABLE 2). During BLAST search in NCBI's GenBank nucleotide database *C. cystidiata* shows only 83% similarity with *C. fuscata*. Morphologically *C. fuscata* differs from *C. cystidiata* in having white coloured

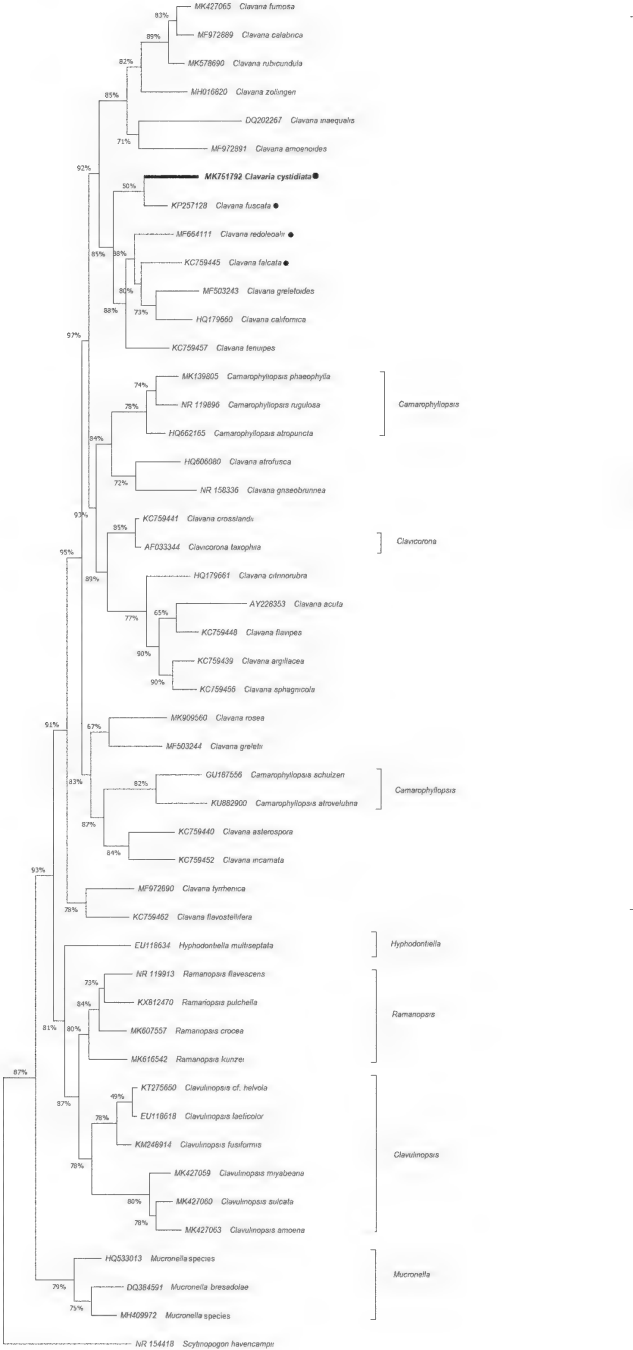




FIG. 3 (left). Maximum likelihood tree showing phylogenetic placement of *Clavaria cystidiata* (shown in bold and with a thickened branch). ML BS values are shown. Sequences are identified by GenBank accession number.

FIG. 4 (above). Bayesian analysis consensus tree for *Clavaria cystidiata* and related taxa, with PP values shown on the branches. Four garlic-smelling species are indicated with asterisks. Sequences are identified by GenBank accession number.

TABLE 2. Morphological comparison between *Clavaria cystidiata* and other garlic-smelling *Clavaria* spp.

	<i>C. cystidiata</i>	<i>C. falcata</i>	<i>C. foetida</i>	<i>C. fuscata</i>	<i>C. redolealii</i>
BASIDIOME COLOR	Pale yellow to yellow	White to cream	Maize yellow	White	White
HYPHAL DIAM (µm)	3–4µm, inflated ≤25	—	6–20	3.5–12	4–12
CYSTIDIA	Present	Absent	Absent	Absent	Absent
SPORE SIZE (µm)	7–10 × 5–8	7–12 × 4–9	5.4–7.2 × 3.2–4.0	8–10 × 4.5–6	6.1–7.6 × 5.4–6.5
BASIDIAL CLAMP	Present	Absent	Absent	Absent	Present
STERIGMATA	2	4	4	2	4
RANGE	Tropical	Tropical & Temperate	Temperate	Temperate	Temperate

basidiomata, absence of basal basidial clamp connections and cystidia, and very small basidia (22–30 µm, Corner 1950). According to Coker (1923), the spore size of *C. fuscata* ranges from 4.4–6 × 8–10 µm. The color of the fruit body and strong garlic odor of *C. foetida* is similar to that of *C. cystidiata*. But spore size (5.4–7.2 × 3.2–4.0 µm), presence of four sterigmata, absence of cystidia, and absence of basal clamp connections of basidia in *C. foetida* (Petersen 1988) separates the two. Unfortunately, *C. foetida* was unavailable for DNA extraction and sequencing for our molecular analyses, as the use of the only known and available single basidiomata of the species deposited in a public herbarium was restricted. Hence, this garlic-smelling taxon could not be included in this study. *C. redolealii* is a garlic-smelling *Clavaria*, having abundant crystalline material in tramal hyphae, with secondary septations and four sterigmata (Petersen 1988). *C. redolealii* also lacks cystidia. These characters differentiate *C. cystidiata* from *C. redolealii*. Sequence of *C. redolealii* showed only 79% similarity with *C. cystidiata* during the BLAST search. Another garlic-smelling taxon, *C. falcata* showed only 80% sequence similarity with *C. cystidiata*. Morphologically, it differs from *C. cystidiata* in having white to cream colored basidiomata, absence of basidial clamp connections, presence of four-spored basidia, and absence of cystidia. *C. cystidiata* is unique from all the described species of *Clavaria* by the presence of its prominent versiform cystidia.

Out of the eight *Clavaria* species described so far with yellowish basidiomata, only one species (*C. amoenoides*) has previously been reported from India (Verma & Pandro 2018). The phylogeny of yellow *Clavaria* species has been studied before. Molecular investigations (Olariaga & al. 2015; Birkebak & al. 2013, 2016) had proved that they do not form a monophyletic group. Our ML and BA studies also support these observations. *C. cystidiata* now ranks as the fifth garlic-smelling species of *Clavaria* to be collected and reported globally. There are no reports of garlic-smelling *Clavaria* species from India to date. Interestingly, our molecular analyses (ML and BA) recovered all taxa with garlic-smelling basidiomata together as a separate group. However, three non-garlic-smelling taxa also are settled in this group. Phylogenetic placement of all other taxa of *Clavariaceae*, included in our analyses, conforms to the results of previous studies (Birkebak & al. 2013, 2016; Olariaga & al. 2015). Our morphological studies and molecular analyses reveal the distinction and phylogenetic placement of *C. cystidiata* within the *Clavariaceae*. Based on these data, we propose the species as new to science.

Key to the *Clavaria* species from India

1. Basidiomata branched 2
1. Basidiomata unbranched 3
2. Basidiomata purple to pinkish purple; frequent to occasional branching *C. zollingeri*
2. Basidiomata white; always with crowded branches *C. jacquemontii*
3. Loop-like clamp connections present at basidial bases 4
3. Loop-like clamp connections absent from basidial bases 5
4. Basidiomata with garlic odor *C. cystidiata*
4. Basidiomata without garlic odor 6
5. Basidiomata yellow *C. amoenoides*
5. Basidiomata not yellow; brown, white, or grey 7
6. Basidiomata pink; basidiospores $6-7.5 \times 4-4.5 \mu\text{m}$, ellipsoid;
hyphae not secondarily septate *C. incarnata*
6. Basidiomata white; basidiospores $8-11 \times 6-8 \mu\text{m}$, globose;
hyphae secondarily septate *C. acuta*
7. Basidiomata brown; basidiospores $5.5-7.5 \times 2.5-3.2 \mu\text{m}$;
basidia $25-40 \times 5.5-8 \mu\text{m}$; hyphae $2-13 \mu\text{m}$ diam *C. indica*
7. Basidiomata white or grey 8
8. Basidiomata grey 9
8. Basidiomata white 10

9. Hyphae inflated 11
9. Hyphae not inflated;
basidiospores $4\text{--}4.5 \times 3\text{--}5 \mu\text{m}$, subovoid, slightly fuscous *C. gollanii*
10. Basidiomata 6.5–8 cm high; basidiospores $3.3\text{--}3.7 \times 5\text{--}7.4 \mu\text{m}$,
ellipsoid, convex on one side; hyphae not inflated, $3\text{--}7 \mu\text{m}$ diam *C. cretacea*
10. Basidiomata 3–10 cm high; basidiospores $4.8\text{--}6.2 \times 3.1\text{--}3.9 \mu\text{m}$,
not ellipsoid, pyriform; hyphae $2\text{--}3 \mu\text{m}$ diam *C. fragilis*
11. Basidiomata 2–3 cm high; basidiospores $4\text{--}6 \times 2.5\text{--}3.5 \mu\text{m}$,
pyriform; hyphae $15\text{--}18 \mu\text{m}$ diam *C. crosslandii*
11. Basidiomata 12 cm high; basidiospores $7\text{--}8 \times 2.8\text{--}6.3 \mu\text{m}$,
subcylindric; hyphae $17 \mu\text{m}$ diam *C. fumosa*

Acknowledgements

The authors thank the Editor-in-Chief Dr. Lorelei Norvell and Nomenclature Editor Dr. Shaun Pennycook for editorial corrections, and Dr. Ivona Kautmanová (Slovak National Museum, Slovakia) and Dr. Anton G. Shiryayev (Ural Division of the Russian Academy of Science, Russia) for providing critical reviews and valuable suggestions for improvement of the manuscript. The authors also thank the Chief Conservator of Forests & Chief Wildlife Warden, Kerala, for permission for fieldwork in the forest areas of Kerala.

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